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THE VEGETATIVE VIGOR OF HYBRIDS AND MUTATIONS.*

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Under what has been termed a kinetic theory of evolution † it has been held that the condition most favorable to evolutionary progress is that found in natural species containing numerous individuals, widely distributed and freely interbreeding. The individual diversity of members of large assemblages of organisms is greater than when interbreeding is confined to narrow limits, but under persistent close breeding uniformity or "fixity" of type is followed, eventually, by very pronounced and abrupt variations, and by a decline of reproductive power.

On the other side of the evolutionary highway corresponding phenomena abound. Interbreeding among the normally diverse members of a species in nature strengthens the organism and aids in distributing variations throughout the species, but when individuals from small, close-bred groups are crossed their characters may prove antagonistic, and not to be combined or averaged in the offspring, as discovered by Mendel. When still more remote types are brought together the resulting hybrids are often abnormally diverse, and may have characters possessed by neither of the parents. Because pronounced variations are thus obtainable both by narrow inbreeding and by wide crossbreeding these extreme stages have been thought to have great

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† Science, N. S., **13**: 969, 1901; Popular Science Monthly, **63**: 18, 1903.

evolutionary significance, but the degenerative character of organisms which have suffered such abnormally abrupt changes is rendered obvious by their inability to propagate their kind.

The partial or complete sterility, both of hybrids and of "sports" or "mutations," as the variations of inbred plants are now called, has long been a matter of common knowledge among breeders of plants and animals, but current evolutionary theories do not associate the two groups of phenomena as belonging to corresponding sidepaths of the evolutionary thoroughfare. The failure to recognize this relationship is to be explained partly by the general carelessness in applying such terms as "hybrid" to a great variety of evolutionary conditions,* and partly by the fact that in spite of their declining reproductive power, both mutations and hybrids often show striking vegetative vigor.

ECONOMIC VALUE VERSUS REPRODUCTIVE FERTILITY.

To recognize and, if possible, to account for this paradox is of practical as well as of theoretical importance, since the propagator, like the biologist, commonly reasons that the more rapid and vigorous the growth of the young plant, the earlier and the larger the harvest. Indeed, this calculation is generally correct, since a large proportion of our domesticated species are not valued for their reproductive efficiency, but for one or another of their vegetative parts. Even in our horticultural crops, such as apples, pears, cherries, plums, berries, oranges, pineapples, and bananas, which we think of as being planted for their fruits, it is not the seed itself which is utilized or desired, but the fleshy pulp. The decline of reproductive fertility, or tendency toward seedlessness, is not looked upon as a disadvantage, if the plant can be propagated asexually, but often lends special value to a new variety, particularly if correlated with vegetative vigor.

The great economic value of a seedless grape or orange need not obscure, however, the obvious fact that the plant itself is degenerate, and would have no prospect of self-perpetuation under natural conditions.† Neither should the utility of some

* Popular Science Monthly, **63**: 225, 1903.

† Mr. Walter T. Swingle notes that in some of the asexually propagated cacti of Arizona vegetative vigor might more than compensate for seedlessness, so that nearly sterile hybrids or mutations would have a distinct advantage over the parental types.

degenerate plants prevent our appreciating the worthlessness of others, or keep us any longer from realizing that methods of breeding calculated to increase the commercial importance of one plant may be utterly destructive to another. A seedless cherry might bring a fortune to its discoverer, but a vigorous and beautiful seedless coffee tree found recently in Costa Rica is of use only in adding emphasis to the fact that all the known variations of this plant which have appeared in cultivation are less fertile than the normal type of the species, and hence are described properly as degenerative, in the original, practical sense of this term, and in its evolutionary sense as well.

SELECTIVE EXPLANATION OF CULTURAL "IMPROVEMENT."

The evolutionary significance of the degeneracy of a large proportion of the domestic varieties of plants and animals has also been obscured by theories that their "improved" characters have been given to them by selection. It is true that the changes have taken place along with a process of selection, but nobody has furnished any tangible reason for believing that the selection causes the changes or can cause them. Neither has it been shown that the new conditions of growth are of much evolutionary significance. The important and practical difference between nature and domestication seems to be that the latter implies narrow inbreeding and the artificial preservation of varieties which in nature would either not appear at all or which would not be able to survive.

The continued popularity of the selective theory and the consequent disregard of the degenerative character of domestic varieties are due, in large measure, to the fact that so many of them possess a vegetative vigor as great or greater than that of the wild type of the species. A sterile hybrid, the mule,* furnishes a popular symbol of strength and hardiness, and scores of similar instances might be enumerated. One of the most striking is Burbank's hybrid walnut tree, which grows several times as fast as either of its parents, but produces no fertile seeds.

*An authentic instance of the fertility of a female mule was encountered last year in the vicinity of Tapachula, in the Soconusco district of the State of Chiapas, Mexico. The colt was alive at birth and apparently normal, but did not survive.

PHYSIOLOGICAL EXPLANATION OF VIGOR OF HYBRIDS.

A physiological explanation of the vigor of sterile hybrids has been sought by supposing that the bodily energy which in other plants or animals goes into reproductive parts and processes here gives a reinforcement of growth, as often occurs after castration. This idea might find some application with the adult organism, but the unusual vigor is often apparent far in advance of the reproductive stage, and even in very young individuals. A nursery of the coffee mutation called "Maragogipe" affords a striking contrast by the side of one planted with the parent "Arabian" type, and a similar precocity of vegetative vigor is found in many hybrids. The diminution of reproductive efficiency is not, evidently, the only difference, and further facts must be taken into consideration if we are to gain a suggestion of how the body of an organism may gain in vigor after the power of perpetuating the type has declined.

THE STIMULATION OF GROWTH BY CROSSING.

The general antithesis between growth and reproduction does not suffice to explain the vigor of sterile hybrids, but by considering the cytological phase of these processes a somewhat more promising clue may be found.

Growth consists, among the higher plants and animals, of a long series of cell divisions, while reproduction requires, on the contrary, a conjugation or union of cells. It has long been supposed that the chief result of fertilization is to stimulate the cell divisions upon which the growth of the new individual depends, and that inbreeding produces defective organisms, because this stimulation is inadequate. Darwin says, for example, that "crossing, by itself, does no good" unless the individuals crossed differ somewhat in characteristics or conditions of growth. Crosses between organisms of a moderate degree of diversity are more vigorous and more fertile than if either of the parent stocks is inbred, but it appears that the limit of fertility is reached much sooner than that of vegetative vigor. This fact corresponds with what has been learned from the microscopical study of cells—that the processes of growth or cell division are much simpler than those involved in reproduction by means of the conjugation of cells. It might be supposed, therefore, that

the vegetative vigor of hybrids is the same phenomenon as the vigor of more normal crosses in spite of their reproductive decline.

KINETIC INTERPRETATION OF VIGOR.

It is not possible, however, to content ourselves with this opinion as complete and final, because it does not take into account the vegetative vigor of mutations, or variations here supposed to be induced by inbreeding, which has been thought to weaken the vegetative as well as the reproductive energies of the organism. Viewed from the standpoint of some of the current theories of evolution, the association of the vegetative vigor of mutations with that of normal crosses and hybrids is certainly not obvious, but the difficulty disappears if we view the question from another standpoint and perceive that the additional vigor may be interpreted in both cases as a phenomenon attending vital motion. Evolutionary progress is accomplished both by new variations and by the combination of those already existing.* Normal crosses and abnormal hybrids and mutations may both be thought of as more vigorous than uniform inbred stocks because they have moved into new positions in the field of development. Variation and cross-fertilization serve the same purpose, and under normal conditions of interbreeding both result in increased vigor and prepotency. The important evolutionary function of cross-fertilization is the mutual communication of variations. Continued variation, change, and diversity are the general tendencies, not uniformity and stability of characters. Organisms are not subject to simple inertia, but, like bicycles and gyroscopes, maintain their equilibrium only when in motion.

Plants often receive an increased impetus of growth by removal to new soils, or by changes of the constituents of the soils through what are significantly called "fertilizers." It is also known that they sometimes respond notably to the presence of small quantities of minerals not used by them, or even to those directly injurious, just as arsenic, prussic acid, and other active poisons serve in medicine as tonics. As a result of a similar stimulation of growth by mineral salts applied to the eggs of some of the lower animals, Professor Jacques Loeb was able to

* "Stages of Vital Motion," Popular Science Monthly, **63**: 14, 1903.

induce a parthenogenetic development which was widely reported two or three years ago as "artificial fertilization."

Cross-fertilization and self-fertility, like most terms, are relative. Many plants have been accounted self-fertile because they can propagate without crossing for a few generations. Thus Wallace has suggested that widely distributed plants are self-fertile, the stimulation of new conditions serving, as it were, as a substitute for crossing. This is doubtless true within limits, but should not be taken to mean that complete autogamy is maintained in this manner.* The effects of new substances and new external conditions, while perhaps to be best understood from the evolutionary standpoint, have not the evolutionary significance often ascribed to them, since the increased vigor and other modifications obtained are neither permanent nor hereditary.

Perhaps for lack of a rational explanation of the known benefits of change of descent or of external conditions, both agriculture and medicine are still practiced largely on the theory that there is some particular food, tonic, fertilizer, or climatic treatment which is best for each plant, animal, or disease. When it is appreciated that even the best is best only while it is recent or new, kinetic systems of farming, feeding, and curing may be elaborated, which shall increase agricultural productiveness and human health by properly determined successions or alternations of diets, tonics, climates, or soils. The rotation of crops, the interchange of seed between different regions, the application of fertilizers, and the breeding of new varieties, more vigorous and resistant, are different methods of attaining the same practical results, and the utility of the several expedients may be found to rest on a single biological law.

The vegetative vigor of hybrids and mutations is not a difficulty, then, in a kinetic theory of evolution, but affords a strongly corroborative series of phenomena. The defective reproduction is the abnormal fact, and this appears to be definitely associated with a lack of normal interbreeding. The organism may be prospered in its growth by any change not

* Mr. Swingle suggests also that the heteroecism of the parasitic rust-fungi may be a phenomenon of the same kind. The diverse forms which the same rust assumes on its different hosts may be looked upon as a further adaptive substitute for interbreeding.

too violent, and its vigor may be increased even by the degenerative variations which follow upon the absence of normal interbreeding. When thus halted or hindered the vital mechanism but turns aside the further because it has lost the equilibrium of normal motion.

It is not necessary to regard variation as abnormal, but the variations which appear under narrow inbreeding and wide cross-breeding are abnormal in their amplitude, like fluctuations of temperature in disease. That even completely sterile mutations and hybrids may enjoy exceptional vigor does not change the fact of abnormality, but shows merely that the evolutionary disorder affects the reproductive rather than the vegetative parts. Both in hybrids and in mutations the tendency to sterility sometimes appears so early that the plants do not produce flowers, or there may be a progressive sterilization of the essential organs of the flowers, as in the so-called "doubling" which has appeared independently in so many mutations of cultivated plants. Others may form apparently normal blossoms in profusion, but set no fruits; fruits may develop without seeds; seeds may be produced which will not germinate, or seedlings may grow, but never mature. There are all possible stages from normal fertility to complete sterility, as there are endless gradations between normal shape and monstrous deformity.

The present interpretation of the facts has at least the merit of simplicity, since it permits us to suppose that the same evolutionary vigor appears in normal variations and crosses, and in abnormal mutations and hybrids, and that the same evolutionary debility affects the two latter conditions. The vigor is due neither to sterility nor to selection, but to variation; the sterility is not explained by normal variation, nor by selection, except as selection implies the absence of normal interbreeding, and the consequent weakening of heredity.

Physiology in the narrower sense, the science of nutrition and other bodily functions, does not explain either the vigor or the debility, but in the broader view evolution itself becomes a physiological process, since it affects not merely the form and structure, but determines also the quality and efficiency of the organism, in quite as practical and definite a manner as do food-supply and other external conditions.